On Myriapod / Insect Interrelationships

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ABSTRACT

In the Tracheata (= Antennata), all non-insect taxa are traditionally classified as "Myriapoda". New insights suggest that this may be mistaken. There is good reason to believe that the Chilopoda form the sister taxon of all other Tracheata. Further, a monophyletic unit formed by all progoneate taxa (Symphyla + Pauropoda + Diplopoda) is the most probable sister taxon of the Insecta (= Hexapoda). Hence, Progoneata + Insecta also form a monophylum. This taxon (sister taxon to the chilopods) is called Labiophora. The insects are maintained as a monophyletic unit. There is no reason to separate the Collembola (as "Parainsecta") from the remaining "true" insects. – Available evidence suggests that the basic phylogenetic branching events in the "myriapods" and also in the insects into higher taxa happened very early, presumably in Late Cambrian/ Early Silurian periods.

RÉSUMÉ

Sur les interrelations entre myriapodes et insectes.

Chez les Tracheata ou Antennata, tous les non-insectes sont traditionnellement considérés comme "Myriapoda". De nouvelles données suggèrent que cela pourrait être erroné. Il y a de bonnes raisons de penser que le groupe Chilopoda constitue le taxon-frère de tous les autres Tracheata. D'autre part, l'unité monophylétique formée par tous les Progoneata (Symphyla, Pauropoda et Diplopoda) est le groupe-frère des insectes le plus probable. Désormais, Progoneata + Insecta forment aussi un groupe monophylétique (taxon frère des chilopodes) appelé Labiophora. Les insectes sont maintenus en tant qu'unité monophylétique, car il n'y a pas de raison d'en séparer les collemboles sous le nom de Parainsecta. On peut valablement penser que l'évènement instituant la base phylogénétique des myriapodes et aussi des insectes parmi les autres grands taxons se produisit très tôt, probablement dans la période Cambrien supérieur - Silurien inférieur.

INTRODUCTION

Most authors, and especially textbook authors, continue to maintain the traditional view that myriapods form a taxon, i.e., a monophyletic unit. But various phylogeneticists feel that a group called "Myriapoda" should be regarded as paraphyletic and therefore be abandoned. Controversial discussions of the question which subtaxon of the so-called Myriapoda might be most closly related to the Hexapoda (= Insecta) go back to the early days of POCOCK (1893) and VERHOEFF (e.g., 1910-1914). On the other hand, the concept of the Myriapoda as a taxon was upheld by HENNIG (1969) and also by BOUDREAUX (1987).

There is no reason to question the monophyletic origin of the Tracheata (= Antennata) as a whole, but this assumption should not be based on the presence of tracheae as a character. Convergent evolution of tracheal systems cannot be excluded and is, perhaps, even probable.

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But there are other, more reliable characters available that should be regarded as autapomorphies of the Tracheata (Fig. 1). For example, the second pair of antennae has been reduced, but its metamere still forms part of the head capsule and is called the intercalary segment. Furthermore, for reasons to be explained below, all tracheates lack a mandibular palpus. In the present paper, we attempt a step-by-step reconstruction of early phylogenetic branching events within the tracheates. In some instances, the fossil record permits estimation of the phylogenetic age of various subtaxa – according to HENNIG's *terminus post quem non* (see e.g., 1969).

MATERIAL AND METHODS

As usual, much of the relevant data is already available and can be derived from previously published papers. Major problems were experienced with reference to the composition of the head capsule and the homology of components of the mouthparts. Specimens preserved in alcohol or BOUIN's fixative were dissected and studied by means of light microscopy (LEITZ interference contrast according to SMITH), and also by scanning electron microscopy (SEM). For light microscopy, chitinous parts were mounted on slides; for embedding, we used HOYER's mixture as this medium has an advantageous light refraction index (for details: see KRAUS, 1984). A camera lucida was used for all drawings.

RESULTS

In this sectio, we deal mainly with uncertainties concerning the composition of the euarthropodean head capsule (see BOUDREAUX, 1987: 120, 121) and investigate various types of mouthparts. The latter part of the investigation is concentrated on the homology of mandibles and on the interpretation of components of the gnathochilarium in Diplopoda and Pauropoda (= Dignatha).

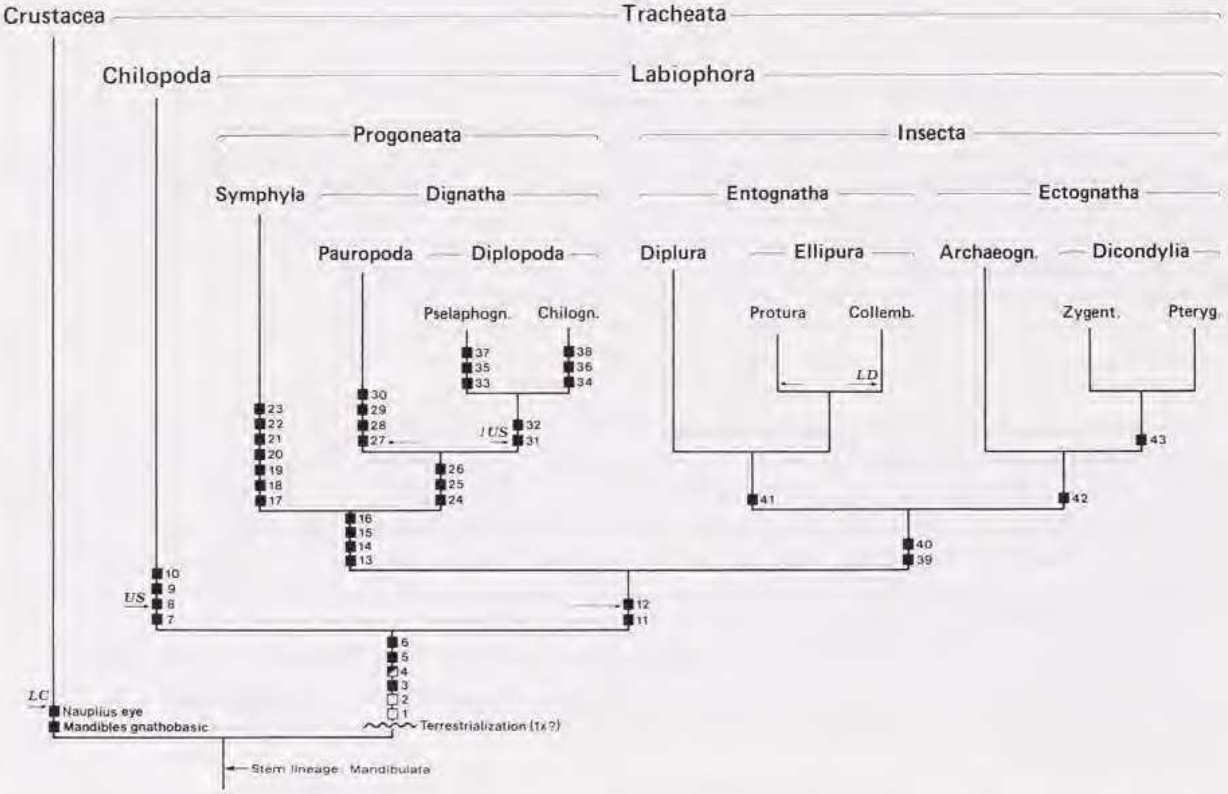


FIG. 1. — Phylogenetic relationships between higher taxa of the Tracheata, their outgroup (Crustacea) included. Arrows indicate age of earliest hitherto known fossils of various groups. — *LC*, Lower Cambrium; *LD*, Lower Devonian; *MD*, Middle Devonian; *US*, Upper Silurian.

Segments of the head capsule

It is now generally accepted that the euarthropodean head capsule includes an acron followed by at least 5 (early fossils), in modern representatives by 6 metameres (LAUTERBACH, 1980a, b; WALOSSECK, 1993: 111). Various authors, however, have believed that the head capsule of the Dignatha is made up of only by 5 metameres. The question arises of whether the regular 6th segment in Pauropoda (TIEGS, 1947: 304) and in at least in Pselaphognatha (Diplopoda) (ATTEMS, 1926: 109) was secondarily excluded from the head capsule *or* whether it had not yet been fully included. A third alternative would be that it *was* and *is* included.

Homology of components of the gnathochilarium

The question of homology is directly concerned with the old problem as to whether the gnathochilarium is made up primarily of the maxillae I *or* by both pairs of appendages, maxillae I and II. VERHOEFF in particular (e.g., 1910-1914), argued that gnathochilaria included two pairs of appendages. This is in contradiction to data derived from ontogenetic studies (DOHLE, 1964, 1980): in the ontogeny of *Glomeris marginata*, the mandibles are followed by only *one* pair of prominent ornaments of appendages. Nonetheless, it remains quite uncertain whether this can be regarded as proof for the assumption that the gnathochilarium does *not* include elements derived from two pairs of appendages.

Pselaphognatha

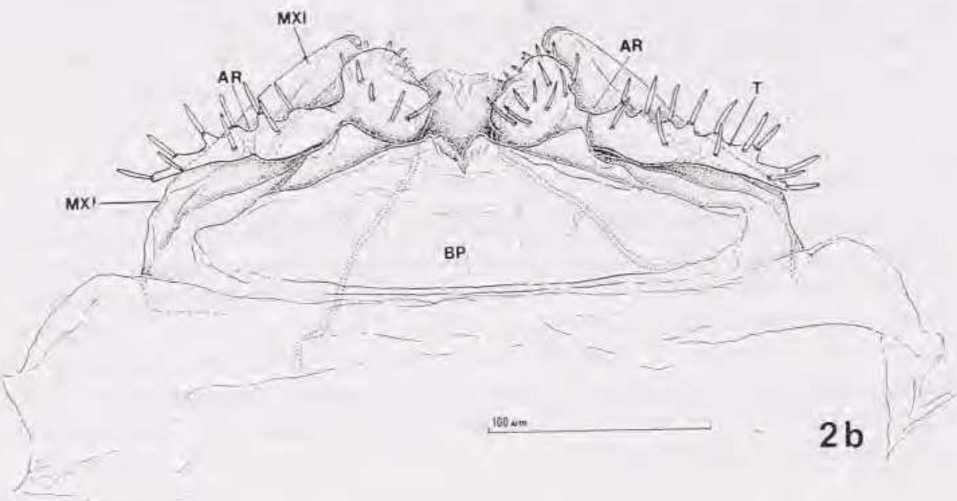
A study of the gnathochilarium in Pselaphognatha seems to supply the key to solution of the problem: there is no gnathochilarium at all in these diplopods! In *Polyxenus,* the mandibles are followed by two (!) pairs of appendages (Fig. 2a, b). The posterior one shows a very broad and partially bipartite basal plate. This piece bears a pair of appendages. They are equipped with numerous sensillae; we interprete them as leg-like telepodites of the maxillae II. Further, the reader is referred to the presence of traces of articulations between segments of these appendages (Figs. 2a). In a somewhat lateral position, another pair of appendages is present in front of these 2nd maxillae and posterior to the mandibles: these parts still show vestiges of segments. We refer to the position of the duct of the "Putzdrüse" (VERHOEFF's term) and interpret these parts as maxillae I. There is no reason to believe that they might be part of the hypopharynx.

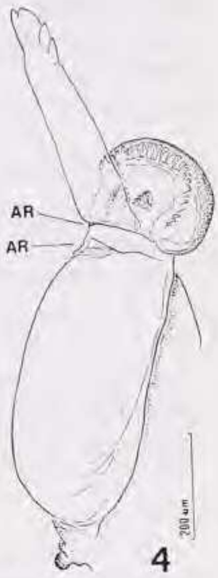
Pauropoda

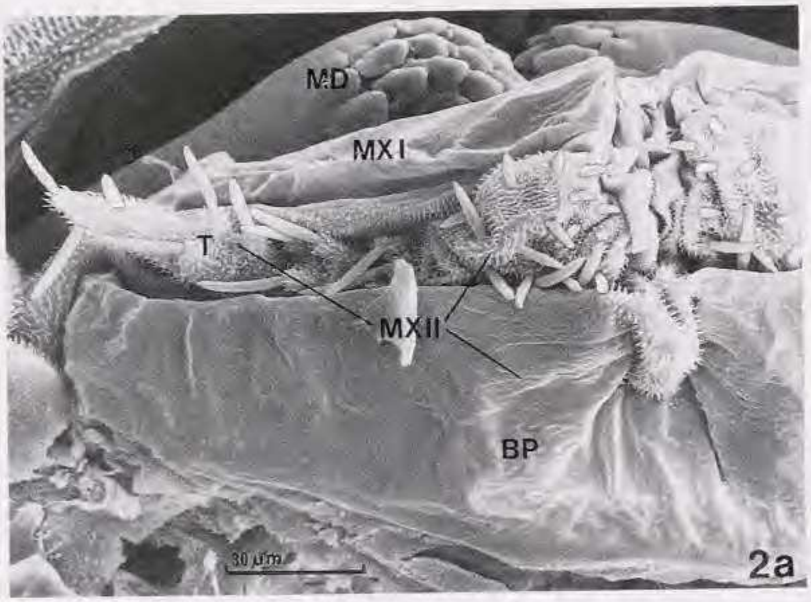
In Pauropods, the head capsule also bears a posterior component which was designated "intermaxillary plate" by TIEGS (1947: 182); this structure does not bear any appendages. In agreement with the arrangement of mouthparts in *Polyxenus*, we interpret the subtriangular plate as representing the maxillae II. In addition, distinct lateral and segmented mouthparts are also present. It was TIEGS (1947), who clearly illustrated their position between the anterior mandibles and the posterior "intermaxillary plate" (see his Fig. 2; also Pl. 3 Fig. 33A). We have studied brachypauropodids and especially Hexamerocerata and can confirm that the position of these paired appendages is between the mandibles and maxillae II (Fig. 3). The obvious interpretation is that they represent the maxillae I. We find it hard to understand how previous authors could invent a pauropodean gnathochilarium (see, e.g., DOHLE 1980: 63, 91).

Chilognatha

Only in the Chilognatha is a true gnathochilarium present, forming the well-known complex unit (VERHOEFF's "Mundklappe") with median and lateral components. In our view, the lateral elements are homologous with the maxillae I and the median elements with the maxillae II (HILKEN & KRAUS, 1994; KRAUS & KRAUS, 1994). Apparently, this development is correlated with the acquisition of new food niches, as the Chilognatha feed on larger food particles than the Pselaphognatha. Accordingly, the "perfect" gnathochilarium should be understood in terms of constructional morphology.







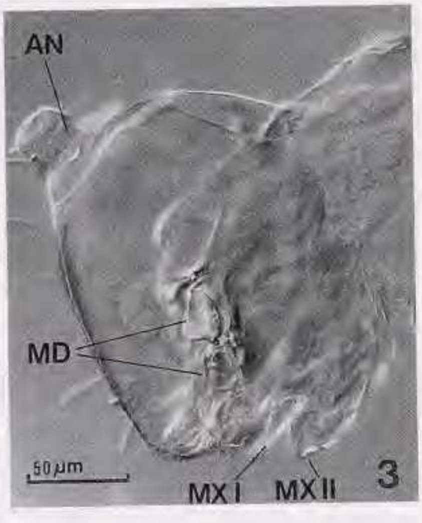


FIG. 2a, b. — *Polyxenus lagurus*, mouthparts. a) SEM-photo, b) drawing. — *AR*, articulations between segments of telopodite, more or less reduced; *BP*, basal plate of maxillae II; *MD*, mandibles, distal part; *MX I*, maxillae I; *MX II*, maxillae II; *T*, telepodites of second maxillae with sensillae.

FIG. 3. — Pauropoda, Hexamerocerata (*Millotauropus silvestrii* Remy, 1953), lateral view of head capsule; *AN*, basis of antenna; *MD*, mandible made up by 3 segments; *MX I*, tip of maxillae I; *MX II*, maxillae II.

FIG. 4. — Archaeognatha (*Trigoniophthalmus alternatus* Silvestri, 1904), telognathic mandible showing vestiges of original articulations (*AR*) between composing segments.

Being fully aware of the fact that this interpretation is in conflict with data derived from ontogeny (DOHLE, e.g., 1980), we argue (i) that there is no other imaginable interpretation of the structures present in postembryonic stages, and (ii) that it is not possible to state definitively that features do not exist on the grounds that they have not yet seen or may even have remained indiscernible during the course of ontogeny. Another, similar, situation concerning the so-called thoracic segments was described by KRAUS (1990). It is now well established that "true" diplosomites with only one pair of legs really exist among the diplopods (see ENGHOFF, 1993)! Hence, one should ask the reverse question: how is it possible that details remain invisible during the course of ontogeny when they are unquestionably present in postembryonic stages?

In conclusion, there seems to be no reason to doubt that the head capsule in Diplopoda and Pauropoda includes 6 metameres – as in all other extant euarthropods.

Mandibles

In all mandibulates, the appendages of the fourth cephalic metamere have been transformed into mandibles. The crustacean mandible is unquestionably gnathobasic (LAUTERBACH, 1972, 1980a). In the ground pattern of the Crustacea, several distal segments of this pair of appendages are accordingly represented by a palp.

On the other hand, there has been much dispute about whether the mandibles in the Tracheata (= Antennata) are also gnathobasic (LAUTERBACH, 1972) *or* – as MANTON believed (e.g., 1977) – telognathous. Attention is drawn to the various types of segmented mandibles in Chilopoda, Symphyla and Diplopoda (see, e.g. MANTON, 1977); the well-known facts on these can be supplemented. MANTON, who made extensive studies of the head capsule in a species of the machilid genus *Petrobius*, did not realize that segment borders are also clearly visible in the mandibles of the Archaeognatha (Fig. 4). The same is true in the Diplura, at least in representatives of the genus *Dinjapyx* (see MARCUS, 1951). This finding is correlated with the absence of a mandibular palp in all tracheate taxa: telognathous mandibles cannot bear a palp!

We therefore have to conclude that the mandibles in the Mandibulata are homologous as far as they correspond to the appendages of the fourth metamere of the head capsule. Their transformation into jaws happened independently, however: they are gnathobasic in the Crustacea, whereas the appendages were suitably modified in the Tracheata as a whole.

DISCUSSION

Reconstruction of phylogenetic branching

There are convincing reasons for believing that the Tracheata are a monophyletic unit:

Combining our results with previously known details and referring to the hypothesis expressed by the present cladogram (Fig. 1) we argue as set out below:

(1) Arthropodia are generally considered as a key character common to all arthropods. This may be questionable. In addition, it is not absolutely certain whether the transition to terrestrial life and the acquisition of uniramous walking legs (LAUTERBACH, 1980a: 147) took place as early as in the stem lineage of the Tracheata as a whole. See character (24).

(2) As in the ground pattern of the Crustacea, the tracheate maxilla II was primarily leg-like (plesiomorphic condition, maintained in chilopods and also in various Pselaphognatha, e.g., *Polyxenus*).

(3) Teleognathic mandibles are part of the ground pattern of the tracheates.

(4) Paired tarsal claws were regarded by HENNIG (1969: 89) as an autapomorphy of the tracheates. This is highly questionable (see, e.g., diplopodean and ellipuran claws).

(5) An intercalary segment presents the third metamere of the head capsule — without appendages.

(6) No digestive mitgut glands have been maintained in all tracheates. Instead, malpighian tubules were developed. Nonetheless, the homology of these organs needs clarification. At

present, the possibility that malpighian tubules evolved more than once, and hence may not be homologous, cannot be excluded.

Chilopoda

(7) The assumed monophyletic origin of the Chilopoda is strongly supported by the transformation of the appendages of the first postcephalic metamere into "maxillipeds" ("Kieferfüsse").

(8) Chilopods are functionally dignathous: their oral cavity is bordered ventrally by the maxillae I; see character (2).

(9) - (10) Reduction of complex eyes to stemmata; loss of median eyes.

Labiophora

(11) The presence of coxal organs, including styli, is assumed to be an autapomorphy of the adelphotaxon to the chilopods: Labiophora. But DOHLE's critical remarks (1980: 86) should be considered.

(12) According to our interpretation of the diplopodean gnathochilarium and of the mouthparts in the Pauropoda, we conclude that in all subordinated taxa the oral cavity is ventrally bordered by a plate formed by the maxillae II. Hence, all representatives of this major taxon are functionally trignathous. The presence of special dorsal organs during the course of ontogeny may constitute another autapomorphy of this group (for details: see DOHLE, 1980: 88).

Progoneata

(13) The anterior position of the genital opening forms a strong autapomorphy of the taxon Progoneata. The opening is constantly located in front of the fourth pair of legs (but the first pair may be reduced).

(14) All progoneates have trichobothria peculiar to this taxon and unknown in all other terrestrial mandibulates. For details see DOHLE (1980: 72).

(15) In contrast to insects, there are no palpi on the maxillae I. It is assumed that the first maxillae are telognathous in progoneates.

(16) Loss of median eyes.

(17) - (23) Symphyla have many autapomorphies. We will mention only a few: genital opening unpaired; special position of a single pair of tracheal spiracles; complete reduction of median and complex eyes; special structure of maxillae II, total loss of telopodites; spermathecae formed by lateral pockets of the mouth cavity; presence of terminal spinning tubules.

(24) All Dignatha have their tracheal spiracles in a ventral position. Internally, they open into tracheal pockets. They also serve as apodems. Such pockets are also present in pauropods (see REMY, 1953: 37).

(25) Reduction of the first pair of postcephalic appendages. Only pauropods have maintained vestiges: "exsertile vesicles" (see TIEGS, 1947: 182, 249).

(26) Presence of "penes" with openings of the vasal efferentia at the tip.

(27) - (30) Pauropoda have many autapomorphies, including specialized antennae; exsertile vesicles [see (25)]; pseudoculus; maxillae II transformed into an unpaired triangular plate.

Diplopoda

(31) Acquisition of diplopody.

(32) Antennae with four sensory cones on tip.

(33), (35), (37) Complex eyes reduced to 5 isolated ommatidia; gnathochilarium with separate maxillae I and specialized telopodites of maxillae II maintained; soft cuticle with conspicuous groups of hairs.

(34), (36), (38) Complex eyes reduced to stemmata; "complete" gnathochilarium; calcification of cuticle; total loss of trichobothria.

Insecta

As far as insects are concerned, we will only mention the presence of a locomotory thorax made up of the postcephalic metameres I to III (39), and the presence of 11 abdominal metameres in the ground pattern (40). A detailed discussion of phylogenetic branching and relationships within the Insecta (= Hexapoda) would not be appropriate here, the reader is refered to the detailed arguments presented in HENNIG's comprehensive work (1981).

PHYLOGENETIC AGE

The geological age of the earliest fossils presently known is indicated in FIG. 1 (arrows). According to phylogenetic branching, the same age must be inferred to equivalent sister taxa. So the presence of Crustacea as early as in Lower Cambrian times indirectly indicates that representatives of the stem lineage of the Tracheata also existed at this period – irrespective of the fossil record. The most important aspect within the Tracheata is the existence of Diplopoda in deposits of Upper Silurian age. This indicates that previous branching events happened earlier, presumably in Upper Cambrian / Lower Silurian times. It is therefore possible to predict that chilopods are considerably older than the earliest known fossil (*Devonobius delta* Shear, 1988).

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